# Increased plasma follicle-stimulating hormone concentrations in prepubertal gilts from lines selected for increased number of corpora lutea

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# Increased plasma follicle-stimulating hormone concentrations in prepubertal gilts from lines selected for increased number of corpora lutea[1,2]

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**ABSTRACT:** Plasma follicle-stimulating hormone (FSH) was evaluated in gilts from two studies in which ovulation rate was increased through direct selection for number of corpora lutea (CL) to determine whether selection for ovulation rate affected FSH secretion during prepubertal development. In the first study, 76 control and 110 selected gilts of University of Nebraska gene pool lines were bled twice during prepubertal development. Plasma FSH concentrations were greater ($P < 0.05$) at 53 (13.5%) and 75 (21.3%) d of age in selected than in control gilts. In the second study, 254 control gilts, 261 gilts from a line selected for ovulation rate, and 256 gilts from a line selected for uterine capacity were bled at three prepubertal ages. Plasma FSH was greater ($P < 0.05$), relative to controls, on d 34 (> 24%), 55 (> 13%), and 85 (> 10%) in White Composite gilts selected for either increased ovulation rate or for greater uterine capacity. Unilateral ovariectomy and hysterectomy were performed at 160 d of age on random gilts in these three lines (n = 377); weights of these organs were evaluated to determine whether selection affected their development. Ovarian and uterine weights were less ($P < 0.01$) in the control than in the ovulation rate line. Subsequently, ovulation rate was determined during pregnancy (n ≥ 130 gilts/line). Controls had fewer ($P < 0.01$) CL (14.6) than gilts of the ovulation rate line (17.7) but numbers similar ($P > 0.10$) to those of gilts of the uterine capacity line (14.7). Within each line, plasma FSH only on d 85 correlated positively with subsequent ovulation rate ($P < 0.03$, 0.001, and 0.08; r = 0.17, 0.30, and 0.15 for control, ovulation rate, and uterine capacity lines, respectively). Ovarian weight at 160 d of age also correlated with subsequent ovulation rate ($P < 0.03$ and 0.001; r = 0.23 and 0.38) in control and ovulation rate gilts but not in uterine capacity gilts ($P > 0.10$; r = 0.11). Gilts selected for increased number of CL, in two independent studies, had greater concentrations of FSH during prepubertal development than respective controls. The modest but significant, positive association of FSH at 85 d of age with subsequent ovulation rate provides additional support for using plasma FSH in prepubertal gilts to indirectly select for ovulation rate.

Key Words: FSH, Ovulation, Selection, Ovarian Development

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## Introduction

The secretion of FSH enhances ovarian follicular growth and development through its receptors on granulosa cells (Nakano et al., 1977; Lindsey and Channing, 1979). Receptors for FSH first appear in primary follicles (Findlay and Drummond, 1999) and become functional in secondary porcine follicles (Morbeck et al., 1993). Concentrations of FSH remain high throughout the luteal phase and decrease during the follicular phase, as follicles grow and secrete more estrogen and inhibin (Hasegawa et al., 1988; Guthrie and Bolt, 1990; Hunter et al., 1996). Although exogenous FSH stimulates follicular growth, subtle differences in endogenous FSH do not account for differences in ovulation rate. In breeds and lines that differ in ovulation rate, no relationship exists between FSH during the follicular phase and subsequent ovulation rate (Hunter et al., 1993, 1996; Mariscal et al., 1998; Wise et al., 2001). However, FSH was greater during the periovulatory period and luteal phase in gilts selected for increased ovulation rate (Kelly et al., 1988; Knox, 1992).

[1]Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable. Research supported by the Nebraska Agricultural Division. Published as Paper No. 13170 Journal Ser. Nebraska Agric. Res. Div.

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Concentrations of FSH are high in prepubertal gilts due to ineffective negative feedback mechanisms (Colenbrander et al., 1987). As puberty approaches, plasma FSH decreases (Diekman et al., 1983; Camous et al., 1985) in association with the appearance of antral ovarian follicles (Oxender et al., 1979). In prepubertal gilts of a line selected for an index of ovulation rate and uterine capacity, plasma FSH concentrations were moderately heritable and positively correlated with subsequent ovulation rate (Cassady et al., 2000). The hypothesis that plasma FSH concentrations during pubertal development are related to ovulation rate was tested in two lines of pigs in which ovulation rate increased in response to direct selection. Ovarian and uterine weights were recorded at 160 d of age in some gilts to examine whether the weight of these organs changed in response to selection.

## Materials and Methods

### *Gilts*

In Exp. 1, blood samples were obtained by venipuncture from each of 186 gilts at mean ages of 53 and 75 d; the range was ± 9.5 d for each age. Gilts were from selected and control lines of the University of Nebraska (**UNL**) Gene Pool population that differed by > 2.5 in mean number of ovulations (Yen, 1999). These two lines were from a 14-breed composite population. Ovulation rate increased in the selected line in response to nine generations of direct selection for number of corpora lutea (Cunningham et al., 1979). The ovulation rate line was then split into two separate lines, one selected at random and the other selected eight generations for litter size (Lamberson et al., 1991). Subsequently, the two selected lines were crossed to form the random litter size (**RLS**) line. The RLS and control lines have been maintained by random selection within line. Gilts (n = 110) from 33 RLS sires were compared with gilts (n = 76) from 19 sires of the control line; they were produced in two consecutive years (n = 91 in the first year and n = 95 in the second). Gilts were weaned at 9 to 13 d of age, placed in a nursery, and at approximately 75 d of age were moved to a finishing building. The second blood sample was collected before relocation to the finishing building.

In Exp. 2, jugular blood samples were obtained from 771 White Composite (equal proportions of Chester White, Landrace, Large White, and Yorkshire breeds) gilts at mean ages of 34, 55, and 85 d; the range was ≤ 7 d for each age. Gilts were the first generation of the terminal evaluation of lines developed through 11 generations of selection for greater number of ovulations or for greater uterine capacity (Christenson et al., 1987; Leymaster and Christenson, 2000). Gilts (n = 254) from 29 sires of the randomly selected control line were compared with gilts (n = 261) from 35 sires of the ovulation rate line and with gilts (n = 256) from 34 sires of the uterine capacity line. All gilts of this generation were randomly selected. The ovulation rate line had a mean of > 3 more ovulations than the other two lines (Leymaster and Christenson, 2000). Gilts were produced in two separate farrowing seasons of the same year (395 gilts were born in March and 376 were born in September). Within each season, piglets were born during a 3-wk farrowing season, weaned at 15 to 20 d of age, placed into a nursery, and then moved into a finishing building after 60 d of age. They were in the finishing building at least 1 wk before their last blood sample was collected. At 154 d of age, gilts in each line were randomly assigned to remain intact and farrow or undergo unilateral hysterectomy/ovariectomy and be slaughtered at 105 d of gestation. At 160 d of age, one ovary and its adjoining uterine horn were removed from each of 377 gilts (Christenson et al., 1987). The side for surgical removal was assigned alternatively. None of the gilts had corpora lutea at 160 d. Excised ovary and uterine horn were trimmed of connective tissue, blotted, and weighed. Each ovary was then pressed firmly between paper towels and weighed again, and the difference in these two weights was used as an estimate of follicular fluid weight. Finally, pressed ovaries were placed in an oven at 45°C, allowed to dry for 48 h, placed in a desiccator for 20 min to allow tissue to return to room temperature, and weighed to obtain a dry tissue weight. Residual fluid weight was wet weight minus follicular fluid weight minus dry weight.

Once-daily estrus detection was begun at a mean age of 209 d. Under this management scheme, age at first estrus could not be determined. Gilts were bred from 8 to 9 mo of age, but none were mated during their first detected estrus. Age at conception averaged 250.4 ± 0.6 d (ranged from 232 to 271 d) and was similar ($P > 0.9$) in all three lines. Thus, there was no indication that lines differed in rate of sexual development. Ovulation rate was determined in intact gilts by counting corpora lutea at laparoscopy on d 36 to 40 of gestation. Ovulation rate in unilaterally ovariectomized and hysterectomized gilts was determined at slaughter at 105 d of gestation. Procedures for handling gilts complied with those specified in the *Guide for the Care and Use of Agricultural Animals in Agricultural Research and Teaching* (FASS, 1999).

### *FSH RIA*

Plasma samples were stored at –20°C until FSH concentrations were estimated by RIA (Krystek et al., 1985; Ford et al., 1997). The antisera was anti-ovine FSH (AFP-C5288113), ovine FSH (AFP-6446C) was used for iodination, and USDA/NIH porcine FSH B-1 was the reference preparation. Interassay coefficients of variation were 8% for a pool of sera from pregnant sows that assayed 235 ng of FSH/mL and 9% for a pool from ovariectomized gilts that assayed 695 ng of FSH/mL.

### *Statistical Analyses*

Plasma FSH concentrations on each day of collection and within each experiment were evaluated separately.

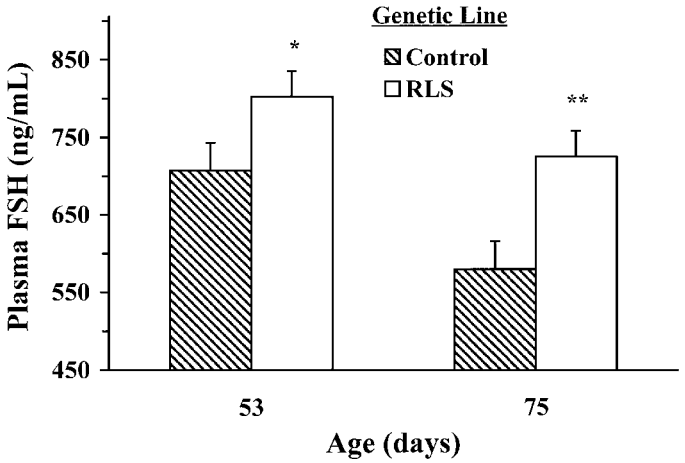


**Figure 1**. Plasma FSH concentrations in prepubertal gilts of the Univ. of Nebraska gene pool lines, controls, and those selected for increased ovulation rate (RLS); *$P$ < 0.05, **$P$ < 0.01 compared with control gilts.

Concentrations of FSH, components of ovarian weight, uterine horn weight, and corpora lutea number were evaluated statistically using mixed model procedures of SAS (Littell et al., 1996). The model contained fixed effects of line and season and their interaction and random effects of sire within line and litter within sire and line. For the FSH data, the age of each gilt on the sample collection day was a covariate. The interaction of season with line did not approach significance for any traits in either experiment ($P$ > 0.20). Control line data were compared with data from the other line(s), and data are presented as mean ± SEM. For the second experiment, the relationships, within line, of plasma FSH concentration, adjusted for age and season, to number of corpora lutea, ovarian weight at 160 d to uterine weight at 160 d, and ovarian weight at 160 d to number of corpora lutea were evaluated by Pearson correlation coefficients (SAS Inst. Inc., Cary, NC).

## Results

In Exp. 1, prepubertal RLS gilts had greater ($P$ < 0.05) plasma FSH concentrations than control gilts on d 53 and 75 of age (Figure 1).

In Exp. 2, gilts from lines selected for increased ovulation rate or uterine capacity had significantly greater plasma FSH concentrations than control line gilts (Figure 2). Differences were significant on d 34, 55, and 85. Gilts of the ovulation rate line had heavier ovaries and uteri than gilts from the control line (Table 1). The difference in total ovarian weight consisted of greater residual follicular fluid and dried ovarian weight (Table 1). Excised ovarian and uterine horn weights were correlated ($P$ < 0.03, r = 0.27, n = 126) at 160 d of age in the ovulation rate line, but these weights were not correlated ($P$ > 0.30) in gilts of the control or uterine capacity line.

Number of CL was greater for gilts in the ovulation rate line ($P$ < 0.01) than for gilts in the control line (Table 1). Within each line, there was no relationship of plasma FSH concentration on d 34 or 55 to number of corpora lutea ($P$ > 0.20). In contrast, plasma FSH on d 85 correlated positively, albeit low, with number of corpora lutea within each line (Table 1). There were 219 gilts with ovarian weights recorded at 160 d of age and ovulation rate determined at slaughter. In these gilts, ovarian weight was correlated with subsequent ovulation rate in the control and ovulation rate lines (Table 1), but not in the uterine capacity line ($P$ > 0.18).

## Discussion

Selection for an increased number of corpora lutea in two unrelated lines of gilts produced greater plasma concentrations of FSH during prepubertal development. From the UNL selection line, Exp. 1, gilts maintained this difference in FSH secretion following a number of generations of relaxed selection. In our second experiment, plasma FSH at 85 d of age correlated with subsequent ovulation rate in all three lines. This phenotypic association existed only at 85 d, when FSH concentrations had begun to decrease in association with the appearance of antral follicles and the maturation of negative feedback regulation of FSH secretion. In contrast, Cassady et al. (2000), with gilts from an independent selection study, reported a significant genetic correlation between ovulation rate and plasma FSH at both 58 and 90 d of age but not at 124 d. This indicates that optimal age to estimate FSH may vary with the genetic line of the gilts. A lack of significant phenotypic correlations, within lines, of plasma FSH on d 34 and 55 with subsequent ovulation rate cannot be explained.

Current observations of line differences in plasma FSH concentrations on d 34 most likely reflect differences in FSH synthesis coupled with subsequent secre-

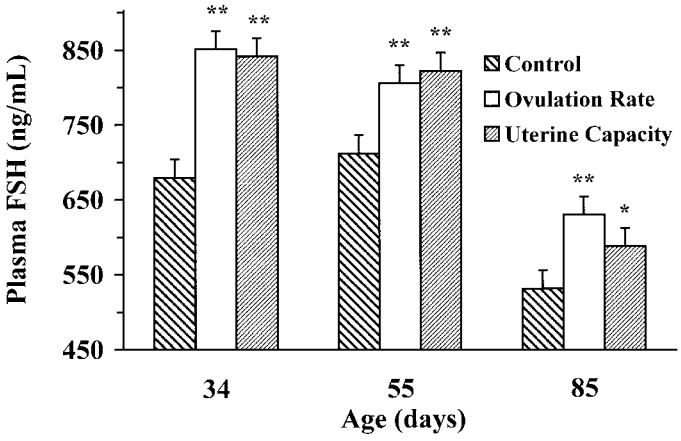


**Figure 2**. Plasma FSH concentrations in prepubertal control gilts and gilts selected for increased ovulation rate or greater uterine capacity during pregnancy, *$P$ < 0.05, **$P$ < 0.01 compared with control gilts.

**Table 1**. Effects of selection on ovulation rate, components of ovarian weight, and uterine weight in White Composite gilts

| Trait | Line | | |
|---|---|---|---|
| | Control | Ovulation rate | Uterine capacity |
| N | 169 | 153 | 130 |
| Number of CL | 14.6 ± 0.3 | 17.7 ± 0.3** | 14.7 ± 0.3 |
| Correlation (d 85 FSH vs no. of CL) | 0.17[b] | 0.30[c] | 0.15[a] |
| 160-d data | | | |
| N | 126 | 126 | 125 |
| Ovarian wet wt, g | 3.17 ± 0.13 | 3.72 ± 0.12** | 2.98 ± 0.12 |
| Follicular fluid wt, g | 1.49 ± 0.05 | 1.62 ± 0.05¶ | 1.38 ± 0.05 |
| Residual fluid wt, g | 1.40 ± 0.07 | 1.74 ± 0.07** | 1.32 ± 0.07 |
| Ovarian dry wt, g | 0.29 ± 0.01 | 0.36 ± 0.01** | 0.28 ± 0.01 |
| Uterine horn wt, g | 24.6 ± 1.1 | 33.3 ± 1.1** | 27.4 ± 1.1¶ |
| N | 80 | 78 | 61 |
| Correlation (d 160 ovarian wt vs no. of CL) | 0.23[b] | 0.38[c] | 0.11 |

¶,*,**Different from control; ¶$P < 0.09$, *$P < 0.05$, **$P < 0.01$.
[a,b,c]Pearson correlation coefficients, [a]$P < 0.08$, [b]$P < 0.05$, [c]$P < 0.01$.

tion. During early postnatal development in gilts, negative feedback regulation of FSH secretion remains inoperative (Colenbrander et al., 1987). These investigators observed similar plasma FSH concentrations in 42-d-old gilts whether gilts were intact or had undergone ovariectomy 5 wk earlier. However, FSH secretion at this age responded negatively to inhibin, administered as charcoal-stripped follicular fluid. Thus, ovaries of 34-d-old gilts likely secrete insufficient inhibin and estrogen to affect plasma FSH concentrations. Consequently, the 24% greater plasma FSH concentrations in gilts of the ovulation rate and uterine capacity lines reflect their greater, intrinsic synthetic capacity on d 34 relative to control line gilts.

As gilts matured beyond 55 d of age, plasma FSH concentrations declined. This reduction reflects greater concentrations of ovarian hormones reaching the pituitary-hypothalamic axis as ovarian follicles mature (Camous et al., 1985; Prunier and Louveau, 1997). Antral follicles first become apparent by 60 to 80 d of age (Oxender et al., 1979; Dyck and Swierstra, 1983) and have greater expression of LH receptors in their theca cells (Nakano et al., 1983; Yuan et al., 1996). After antral formation, follicles grow at a faster rate, granulosa cells secrete greater quantities of steroids and gonadotropin dependence shifts from FSH to LH (Guthrie et al., 1988; Morbeck et al., 1992; Draincourt et al., 1995; Yuan et al., 1996). A progressive decline in sensitivity of the pituitary/hypothalamic axis to negative feedback by gonadal steroids, the gonadostat hypothesis, characterizes the regulation of LH secretion during pubertal development in many mammals (Goldman, 1981). Gilts align with this hypothesis; they require more estradiol, adjusted for increasing body weight, to suppress LH secretion as they age (Berardinelli et al., 1984). This relationship occurs in association with a declining rate of estradiol clearance from the systemic circulation (Elsaesser et al., 1982; Christenson et al., 1985).

In all three lines, positive correlation of FSH with subsequent number of CL was not detected until FSH secretion decreased in association with pubertal development. The basis for greater plasma FSH in prepubertal gilts that subsequently have a greater number of CL remains to be determined. Points to consider include ovarian follicular status at 85 d, biological activity of FSH, clearance from the circulation, and sensitivity of hypothalamic/pituitary axis to ovarian feedback. An evaluation of ovarian morphology at 85 d of age will influence the direction of future studies. Regardless of its mechanism of regulation, these findings support the use of prepubertal plasma FSH concentrations to select for improved ovulation rate in pigs, albeit a modest phenotypic relationship. Cassady et al. (2000) predicted that selection based on pubertal FSH concentrations in both boars and gilts would be 93% as effective as direct selection in gilts for number of corpora lutea. To add perspective to the current results, we could cull the 25% of gilts from each line that had the lowest plasma FSH on d 85. The mean number of CL for the remaining 75% of gilts would be 1.1, 1.7, and 1.0 greater for control, ovulation rate, and uterine capacity gilts, respectively, than the means for the culled gilts. A selection scheme based on FSH concentration would eliminate costly surgical intervention.

Elevated FSH during prepubertal development was not genetically associated with greater ovulation rate in all lines. Gilts selected for greater uterine capacity had greater plasma FSH concentrations but similar ovulation rate compared with controls; thus, prepubertal FSH secretion did not influence subsequent ovulation rate. Porcine follicles do not respond to exogenous gonadotropins at 34 d of age but acquire responsiveness to gonadotropins with increasing age (Casida, 1935; Oxender et al., 1979; Pressing et al., 1992). Presently, we can only predict that selection for greater uterine capacity increased prepubertal plasma FSH concentrations through effects of pleiotropy (single gene having

multiple effects) and(or) genetic linkage. In a separate line of gilts, significant evidence of QTL for ovulation rate as well as suggestive evidence of a second, unlinked QTL for uterine capacity were identified on chromosome 8 (Rohrer et al., 1999). The possibility of selecting for greater FSH concentrations without having an effect on ovulation rate cannot be ignored.

In spite of the disparity in FSH concentrations on d 34 and 55 between the uterine capacity and control lines, FSH on d 85 was phenotypically correlated with ovulation rate in both lines. These correlations were less than the correlation in the ovulation rate line. Thus, as ovulation rate increased in gilts through direct selection, this trait apparently became more strongly associated with prepubertal FSH secretion. Likewise, gilts of the ovulation rate line had greater phenotypic correlations of 160-d ovarian weight with 160-d uterine horn weight and 160-d ovarian weight with later ovulation rate than the control or uterine capacity lines. Due to the observed line differences in ovarian and uterine horn weights at 160 d, subsequent research must directly assess age at puberty to test the assumption that these lines do not differ in this regard. Collectively, current findings support the conclusion that selection for ovulation rate increased prepubertal plasma concentrations of FSH in gilts (Cassady et al., 2000).

## Implications

Plasma follicle-stimulating hormone concentrations during prepubertal development were greater in gilts selected for increased ovulation rate in two independent studies. Furthermore, in 85-d-old gilts of the second study, plasma follicle-stimulating hormone concentrations were correlated positively with subsequent ovulation rate in three lines, but this association was greatest in gilts of the ovulation rate line. Collectively, these findings provide additional support for the use of plasma follicle-stimulating hormone concentration to indirectly select for ovulation rate in swine.

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